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Cephalopods Occupy the Ecological Niche of Epipelagic Fish in the Antarctic Polar Frontal Zone

PAUL G. RODHOUSE AND MARTIN G. WHITE

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK

Recent data from research cruises and exploratory fishing in the Antarctic Polar Frontal Zone (APFZ) of the Scotia Sea, together with data from dietary studies of Antarctic vertebrate predators, have revealed a large, previously overlooked trophic system in the Southern Ocean (Fig. 1). The upper trophic levels of this open-ocean epipelagic community are exceptional in that they contain no fish species. Fishes are replaced by cephalopods, including the ommastrephid squid, Martialia hyadesi. *This squid preys on mesopelagic myctophids (lanternfish), which feed largely on copepods. We identify here a geographically distinct, Antarctic, open-ocean food chain which is of importance to air breathing predator species but where Antarctic krill,* Euphausia superba, *is absent. This system is probably prevalent in areas of higher primary productivity, especially the Scotia Sea and near the peri-Antarctic islands. Squid stocks in the APFZ may have potential for commercial exploitation, but they, and the predators they support, are likely to be sensitive to overfishing. Squid have a short, semelparous lifecycle, so overfishing in a single year can cause a stock to collapse.*

The presence of this trophic system was already evident among the results of the *Discovery* expeditions. Large quantities of squid remains, especially their indigestible beaks, were found in the gut contents of several albatross and seal species (1). But because *E. superba* is so conspicuous and plays such an important role in the diet of vertebrate predators (especially commercially exploited baleen whales), and as these crustaceans were amenable to marine biological research methods of the day, the cephalopod trophic system in the vast but remote region of the APFZ was largely ignored.

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Abbreviations: APFZ = Antarctic Polar Frontal Zone; BAS = British Antarctic Survey.

Following a review of the resources of the Southern Ocean (2) that noted the possible presence of large cephalopod stocks, studies of the cephalopod prey of vertebrate predators breeding at South Georgia (Fig. 2) in the 1970s (3) revealed that an unidentified ommastrephid, *Todarodes?* sp. dominated the diet of some species. Collections of cephalopod remains in the predator regurgitations at South Georgia (4,5) made in the 1980s by scientists of the British Antarctic Survey (BAS), coincided with a large "by-catch" of the little-known ommastrephid *M. hyadesi* in the new fishery for the squid *Illex argentinus* on the Patagonian Shelf during 1986 (6). A comparison of material from both sources revealed that the species being taken by predators, previously identified as *Todarodes?* sp., was *M. hyadesi*. Exploratory fishing by Japanese squid jiggers in the APFZ west of South Georgia subsequently caught commercial quantities of *M. hyadesi* near the surface (<50 m), confirming the presence of this species in the Scotia Sea (6). Although stock size cannot be assessed at present, annual predator consumption of *M. hyadesi* in the region is estimated at >330,000 tonnes (7). Stomach contents of jigged specimens showed they had fed on a community of myctophid fish dominated by *Krefftichthys anderssoni* (8). Myctophids feed largely on copepods, so this food chain may be partially or fully independent of the *Euphausia superba* trophic system. Elsewhere in the APFZ, myctophids have recently been identified as the major food resource for other higher predators such as the king penguin (9).

During the 1994 research cruise of RRS *James Clark Ross* (BAS) satellite-tagged albatross predators of *M. hyadesi* and other squid were tracked to the APFZ, north of South Georgia; there the pelagic community exploited by the birds was sampled with a commercial trawl. The samples included the squids *M. hyadesi*, *Moroteuthis knipovitchi* (the major prey of southern elephant seals), *Go-*

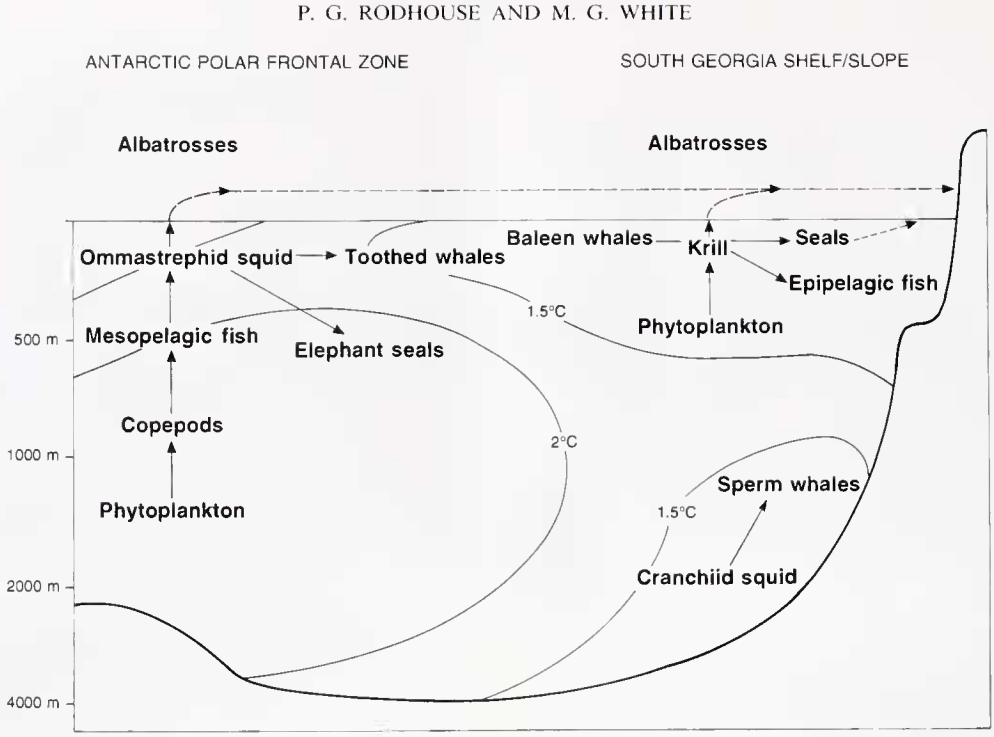

Figure 1. Spatial relationship between the myctophid/cephalopod trophic system at the Antarctic Polar Frontal Zone and the *Euphausia superba* based system on the South Georgia shelf and slope (positions of organisms in the water column do not represent their bathymetric distribution).

natus antarcticus, *Galiteuthis glacialis*, and *Brachioteuthis* sp. (Rodhouse, P. G. *et al.*, BAS, in prep). The data confirmed that, in the Southern Ocean, in the vicinity of the APFZ, *M. hyadesi* occurs near the surface (<100 m). Albatross predators breeding at South Georgia and large male sperm whales feeding in the vicinity of the islands (10) exploit different, geographically separated, cephalopod communities. The whales' diet does not include significant numbers of *M. hyadesi;* rather it is dominated, in terms of biomass, by the gigantic Antarctic cranchiid squid, *Mesonychoteuthis hamiltoni*.

The biological oceanography of the APFZ is poorly understood. Primary productivity in the ice-free zone of the Southern Ocean is generally low (11). Strong westerly winds generally maintain a deep mixed layer, but composite Coastal Zone Color Scanner images reveal regions of high concentrations of phytoplankton pigment, indicating enhanced productivity in the Scotia Sea, in the vicinity of the Scotia Arc, and near the peri-Antarctic islands (12). In the ice-free zone of the Scotia Sea, the pelagic community is dominated by copepods, small euphausiids, gelatinous zooplankton, and myctophids (13,14). Elsewhere in the APFZ, *M. hyadesi* has been recorded from the Kerguelen (15) and Macquarie (16) islands, suggesting that this squid occurs in areas of enhanced productivity in the pelagic community.

The composition of the Antarctic pelagic fish community is unusual by comparison with such communities in other oceans, because epipelagic fish families are absent. Key components of the pelagic food-web in temperate and tropical seas—clupeids, carangids, scombrids and their predators, the oceanic sharks—are absent or rare vagrants on the periphery of the Southern Ocean. At shallow depths around the Antarctic Continent and the peri-Antarctic islands, demersal fish, mostly members of the endemic suborder Notothenioidei, dominate the fish fauna. Most species are demersal as adults, but a small number, notably *Pleuragramma antarcticum* near the continent and *Champsocephalus gunnari* in the vicinity of islands, have become secondarily adapted to inhabit pelagic habitats. Others are temporarily pelagic during early ontogeny. By contrast, the fish fauna of the open ocean is limited to deepwater bathypelagic and mesopelagic species. Of these, the myctophids predominate, and are sufficiently abundant to support a fishery (17). In the north Scotia Sea, mesopelagic fish, mainly myctophids, constitute up to 18% of the total nekton biomass and are the main component of the biomass available to higher predators (13,14). But epipelagic fish are absent, and we now conclude these are replaced by a cephalopod community dominated by ommastrephid squid.

An epipelagic system dominated by cephalopods is possibly the consequence of physiological constraints on fish in cold sub-Antarctic or Antarctic waters, that do not apply to the cephalopods; or may have arisen because the life cycle traits of cephalopods may be better adapted to

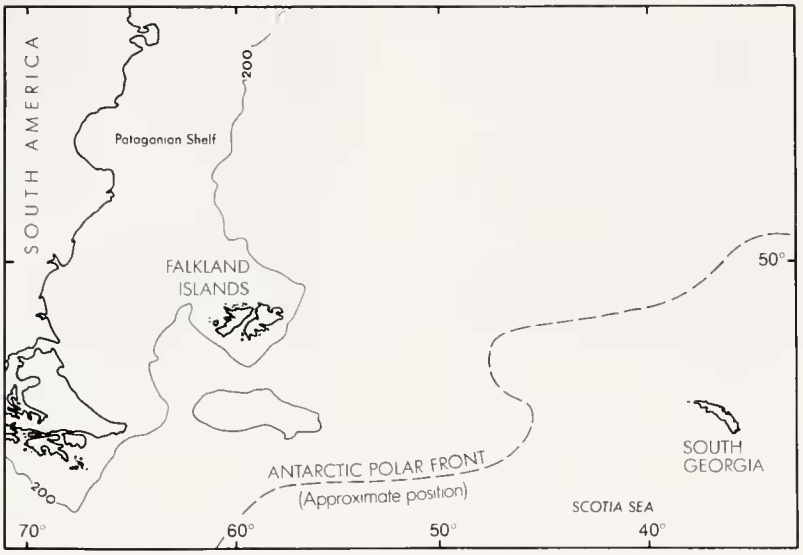

Figure 2. Atlantic sector of the Southern Ocean showing the position of South Georgia and the Antarctic Polar Front.

the physical environment of the APFZ. The relatively short life span of cephalopods might allow them to complete the life cycle, at least from the planktonic to the nektonic phase, before they are flushed out of productive regions by the fast-flowing Antarctic Circumpolar Current. If epipelagic communities in other remote oceanic regions are similarly dominated by cephalopods, then comparative studies may shed light on these questions.

As finfish stocks have declined globally, cephalopod catches have grown and, in terms of dollar value of the catch, are currently rated third in world importance after shrimp and tuna (18). Pressures on fish stocks continue to increase, and conflict at sea between fishing nations is likely to escalate in the absence of political will to reduce fishing effort. Under these circumstances, new cephalopod stocks are likely to be sought as an alternative, high-value resource. Stocks of *M. hyadesi* straddle the region administered by the Commission for the Conservation of Antarctic Marine Living Resources, and the high seas to the north. This will complicate management of any future fishery in the region. Given the important role of cephalopods in the diet of several species of higher predator in the Antarctic (19) and the vulnerability of short-lived, semelparous species to overexploitation, the ecological consequences of an unmanaged fishery for cephalopods in the Southern Ocean are potentially severe.

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